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Establishing the nutritional landscape and macronutrient preferences of a major United States rangeland pest, *Melanoplus sanguinipes*, in field and lab populations

Deanna Zembrzuski[1], Derek A. Woller[2], Larry Jech[2,3], Lonnie R. Black[2], K. Chris Reuter[2], Rick Overson[1,4], Arianne Cease[1,4]

1 School of Life Sciences, Arizona State University, Tempe, AZ, USA.
2 USDA APHIS PPQ Science & Technology Insect Management and Molecular Diagnostics Laboratory (Phoenix), Phoenix, AZ, USA.
3 Tempe, USA.
4 School of Sustainability, Arizona State University, Tempe, AZ, USA.

Corresponding author: Deanna Zembrzuski (dzembrzu@asu.edu)

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Abstract

When given a choice, most animals will self-select an optimal blend of nutrients that maximizes growth and reproduction (termed "intake target" or IT). For example, several grasshopper and locust species select a carbohydrate-biased IT, consuming up to double the amount of carbohydrate relative to protein, thereby increasing growth, survival, and migratory capacity. ITs are not static, and there is some evidence they can change through ontogeny, with activity, and in response to environmental factors. However, little research has investigated how these factors influence the relative need for different nutrients and how subsequent shifts in ITs affect the capacity of animals to acquire an optimal diet in nature. In this study, we determined the ITs of 5th instar (final juvenile stage) *Melanoplus sanguinipes* (Fabricius, 1798), a prevalent crop and rangeland grasshopper pest in the United States, using two wild populations and one lab colony. We simultaneously collected host plants to determine the nutritional landscapes available to the wild populations and measured the performance of the lab colony on restricted diets. Overall, we found that the diet of the wild populations was more carbohydrate-biased than their lab counterparts, as has been found in other grasshopper species, and that their ITs closely matched their nutritional landscape. However, we also found that *M. sanguinipes* had the lowest performance metrics when feeding on the highest carbohydrate diets, whereas more balanced diets or protein-rich diets had higher performance metrics. This research may open avenues for studying how management strategies coincide with nutritional physiology to develop low-dose treatments specific to the nutritional landscape for the pest of interest.

Keywords

geometric framework, macronutrient preference, nutritional ecology, nutritional landscape, plant–insect interactions, rangeland grasshopper

Introduction

Rangelands in the western United States are important agricultural and environmental resources, serving not only as grazing lands for livestock, but also as habitats for wildlife (Havstad et al. 2007). While the U.S. has not been home to a locust species since the 1870s [the extinct Rocky Mountain locust, *Melanoplus spretus* (Walsh, 1866) (†), originally described within *Calopteneus* by Walsh in 1866, see Lockwood 2004], the rangelands are sometimes plagued by large grasshopper outbreaks (Capinera and Sechrist 1982, Joern and Gaines 1990, Schell and Lockwood 1997). Grasshoppers represent a significant problem for ranchers and farmers across the United States, but especially in the western rangelands (Hewitt and Onsager 1983). Grasshopper outbreaks can represent a significant economic hardship to ranchers, with conservative estimates placing the economic damage of grasshoppers at $393 million in rangeland forage lost annually (Hewitt and Onsager 1983). There is support for the use of fungal management for rangeland grasshoppers (Streett 1996–2000, Bidochka and Roberts 2000, Branson et al. 2006), and nutritional ecology can be helpful when applying these management strategies. However, few studies have bridged lab and field research to understand how the nutritional requirements of grasshoppers relate to the host plants available to them in the field.

In rangelands, the migratory grasshopper *M. sanguinipes* (Fabricius) is the most destructive grasshopper, causing more forage loss than any other grasshopper species in the United States (Pfadt 2002). This grasshopper is not exceptionally large, with a body length of approximately 16–23 mm for 5th instars, 20–26 mm for adult males, and 20–29 mm for adult females (Pfadt 2002).

Management of this species is particularly challenging because populations that emerge in rangelands can then migrate to croplands miles away. Due to their mixed (grasses and forbs) feeding behavior, they will consume vegetables in addition to cereal crops and grasses (Pfadt 2002, Murray 2016). Indeed, as described in COPR (1982), this species is "decidedly ambivorous" and will "devour and thrive on almost any available plant," including plants from grasslands and crops to hedge mustard and moss. This grasshopper is especially problematic because of its large outbreak potential, with outbreak populations able to reach 80 individuals/yd^2 (Murray 2016). Due to its economic impact, *M. sanguinipes* has often been the subject of population management research (Pickford and Mukerji 1974, Hewitt 1977, Hewitt and Onsager 1983, Pfadt 2002), as well as nutritional and life history studies (Behmer and Joern 2008, Fielding and Defoliart 2008). However, there is still much unknown about this major rangeland pest species' nutrient preferences in field populations and how those compare with long-term lab colonies.

When given a choice, most animals will self-select the blend of nutrients that maximizes growth and reproduction (termed "intake target" or IT), which arises from the Geometric Framework for Nutrition, or GFN (Raubenheimer and Simpson 1997, Raubenheimer et al. 2009, Simpson and Raubenheimer 2012). GFN research spans many taxa and has demonstrated that numerous insect populations, particularly lab colonies, exhibit a consistent IT. For example, *Plutella xylostella* (Linnaeus, 1758) caterpillars select a macronutrient ratio similar to ancestral colony conditions (3.25 mg protein: 3.00 mg carbohydrates), and that ratio corresponds with a narrow and high peak in performance (Warbrick-Smith et al. 2009). Several migratory grasshopper and locust species select a carbohydrate-biased IT, consuming up to double the amount of carbohydrate relative to protein, which increases growth, survival, and migratory capacity (Behmer and Joern 2008, Cease et al. 2012, 2017, Le Gall et al. 2019, Le Gall et al. 2020a, b, Talal et al. 2020).

ITs are dynamic, and there is some evidence they can shift through ontogeny, with activity, and in response to environmental factors (Raubenheimer and Simpson 1997, Simpson and Raubenheimer 2012, Lawton et al. 2020). There is also evidence that meeting an IT not only maximizes growth performance under optimal conditions, but also aids in survival when faced with toxins and pathogens. *Helicoverpa armiger* (Hübner, 1808) and *Helicoverpa punctigera* (Wallengren, 1860) caterpillars fed on diets that match their IT have lower susceptibility to several *Bt* toxins (Tessnow et al. 2018). *Chortoicetes terminifera* (Walker, 1870), the Australian plague locust, adjusts its IT when faced with a pathogen challenge, and the adjusted IT reduces the grasshopper's susceptibility to the pathogen (Graham et al. 2014). Given how important external factors are on ITs, little research has investigated how these factors influence the relative need for different nutrients and how subsequent shifts in ITs affect the capacity of animals to acquire an optimal diet in nature.

The GFN has been used to analyze long-term and first-generation lab colonies of *M. sanguinipes*. For example, one lab study on 5th instar first-generation lab-reared grasshoppers collected from Arapaho Prairie (Arthur Co., Nebraska) showed that *M. sanguinipes* had a 1:0.96 preferred dietary ratio of protein to carbohydrate (p:c) (Behmer and Joern 2008). Results from another study on two 2nd generation lab populations of grasshoppers from Alaska (1p:0.90c) and Idaho (1p:0.95c) suggested that the ITs of both populations remained similar, though the Alaska population regulated more tightly than the Idaho grasshoppers (Fielding and Defoliart 2008). However, no studies have examined macronutrient preferences of *M. sanguinipes* collected directly from field populations. Understanding how an organism's nutritional requirements compare to their habitat's macronutrient composition can aid in developing management strategies based on nutrition (e.g., Cease et al. 2015, Le Gall and Tooker 2017, Word et al. 2019, Le Gall et al. 2020a).

The primary goals of this study were to 1) compare the IT of two field populations of *M. sanguinipes* to their given nutritional landscape, 2) compare the IT of these two field populations to the IT of a long-term lab colony, and 3) determine if the lab colony IT maximized performance by restricting grasshoppers to one of five diets varying in p:c ratio. Our null prediction was that a given field population of grasshoppers would have an IT that roughly matched the protein and carbohydrate ratios of plants available to them. We predicted that, relative to the long-term lab colony, the field populations would be more carbohydrate-biased, similar to other field populations of migratory acridids (Cease et al. 2012, Le Gall et al. 2020b, Lawton et al. 2021), perhaps due to increased activity or stressors. Finally, we hypothesized that grasshoppers select a diet that provides optimal performance and, thus, predicted that the p:c ratio of the diet on which the lab colony performed the best in restricted diet experiments would be similar to the lab colony IT.

Methods

Field population studies

Studied species and studied area.—*M. sanguinipes* is an abundant rangeland grasshopper with a range that extends throughout most of the United States and into Canada (Pfadt 2002, Otte 2013). This grasshopper has 5–6 nymphal instars, and nymphal development takes 35–55 days. The 5th instar is easily recognized by the wing buds shifting from small buds on the side to larger buds along the dorsal side of the grasshopper (Pfadt 2002). We consulted with USDA surveyors in Idaho to determine locations with sufficient populations of *M. sanguinipes* for this study. Based on their surveys, we selected two locations. Location 1 was a 3.9 ha plot of Bureau of Land Management (BLM) cattle grazing land in Bliss, Idaho (see Table 1 and Suppl. material 1: Fig. S6 for specific locations) and was mostly dry rangeland with forbs, some light woody vegetation, and an abundance of grasses. Location 2 was a 1.2 ha plot of private non-grazed property in Boise, Idaho (see Table 1 and Suppl. material 1: Fig. S7 for specific locations). The vegetation was not irrigated and had a similar plant community composition to Bliss. Grasshoppers were collected from the field in 2018 on June 26 for Bliss and July 2 for Boise.

Plant collection.—We sampled plants from each location concurrent with the sampling of grasshoppers. We randomly selected five collection plots per site using a random number generator. Plots were 5 m × 5 m, and we mapped the plots for each location using Google Maps (2021a, b) (Suppl. material 1: Figs S6–S7). In each plot, we visually estimated the percent ground cover at ground level for grasses, forbs, and shrubs using the relevé method (Poore 1955, Minnesota Department of Natural Resources 2013). We measured humidity, wind speed, and temperature at each plot with a digital anemometer (Ambient weather WM-4). To broadly assess the nutrient contents of the plots, we collected living leaf material (the part generally eaten by grasshoppers) eaten by the most abundant species from each functional group. Some plant species were completely dead in a plot and were not collected. Plants were stored in paper bags, air-dried for three days, and then further dried for another 24 hours in a 60 °C oven.

Grasshopper collection.—We collected grasshoppers throughout the field locations using sweep nets. All specimens were identified to species by KCR, who has over 40 years of experience with the identification of rangeland grasshopper species. We recorded the sex and developmental stage of grasshoppers upon capture, and early 5th (final) instar grasshoppers were kept for the experiment. We separated grasshoppers by sex and kept them in separate cages with a selection of plants wrapped in wet paper towels from the collection site for 24 hours prior to starting experiments. All collected specimens were then brought to a private ranch southeast of Boise for the experiments.

Intake targets.—We started IT experiments for field populations on June 27 for Bliss and July 3 for Boise. To determine self-selected ITs, we used a restricted diet choice experiment that gave grasshoppers a choice between two complementary diets. We had two treatment groups where one diet was kept constant between the two treatments and the other diet had a variation in the protein and carbohydrate ratio so we could ensure the ITs were not a result of random eating. Twelve male and 12 female grasshoppers were placed into each treatment group for a total of 48 grasshoppers from each population. Both treatments received two complementary (high protein (p): low carbohydrate (c) and low p: high c) isocaloric diets. By percentage of dry mass, Treatment A contained 7p:35c and 28p:14c, while Treatment B contained 7p:35c and 35p:7c. We selected these two different diet pairings so we could determine if grasshoppers were regulating to a specific p:c ratio; if so, grasshoppers from both treatment A and B would end up selecting the same p:c ratio, regardless of their diet pairings. This range of dietary p:c pairings encompassed all but a couple of the most carbohydrate-biased plants, meaning that grasshoppers could reach the same IT on the artificial diets as they could eating field plants. Diets were made based on Dadd (1961) and as modified by Simpson and Abisgold (1985). The protein was a 3:1:1 mix of casein, peptone, and albumen; the digestible carbohydrate (hereafter, carbohydrates) was a 1:1 mix of sucrose and dextrin. All diets contained similar amounts of Wesson's salt (2.4%), cholesterol (0.5%), linoleic acid (0.5%), ascorbic acid (0.3%), and vitamin mix (0.2%).

At the start of the experiments, we weighed the grasshoppers and placed them into individual plastic cages (17.5 × 11.8 × 4.3 cm), perforated for airflow and with a water tube and the two diet dishes. Five extra cages without grasshoppers were set up containing a dish of each of the three diets and a water tube to record water mass gained by the diet during the experiment. The grasshoppers were in their treatment for 48 hours in Bliss (ended early due to high mortality) and 72 hours in Boise. We checked the cages daily and recorded any mortality or molting, and additional water was added as needed. Grasshoppers that died during the experiment were not included in our final analyses. At the conclusion of the experiment, we recorded grasshopper mass. We weighed the diet dishes before and after the experiment and calculated the amount of protein and carbohydrate consumed by each grasshopper, accounting for any water mass gain in the diets by adjusting the initial weights of the diets based on the average proportion change found in the diets kept in the extra five cages.

We recorded temperature and relative humidity in the cages using iButtons (Thermochron, Maxim Integrated). Cages were kept inside a garage on, approximately, a 15h/9h light/dark cycle directly correlating to the natural light/dark cycle at the time and at ambient shade temperature. For the Bliss experiments, the average daytime (6:10 am–9:30 pm) temperature and humidity +/- SEM were 24.18 +/- 0.26°C and 27.18% +/- 0.53% and average nighttime (9:31 pm–6:09 am) values were 24.50 +/- 0.21°C and 27.64% +/- 0.40%. For the Boise experiments, daytime averages were 25.87 +/- 0.22°C and 22.94% +/- 0.43%; nighttime averages were 24.86 +/- 0.22°C and 28.37% +/- 0.66%.

Chemical analyses.—For each vegetation survey 5 m × 5 m plot, we mixed leaves from plants of the same functional group (grasses and forbs) together and ground them into a fine powder using a ball mill (30 s at 30 Hz using a Retsch MM 400 ball mill) for a total of 5 samples per functional group per field site. The carbohydrate content of each sample was determined using the phenol-sulfuric acid carbohydrate assay (DuBois et al. 1956), and the protein content was determined using the Bradford protein assay (Bradford 1976). Shrubs were excluded from the analyses, as they do not typically make up the natural diet of this grasshopper (Pfadt 2002).

Lab studies

Lab colony.—The Arizona State University *M. sanguinipes* lab colony used in these experiments originally came from eggs from a USDA ARS lab colony based in Sidney, MT. The USDA colony was established in approximately 1970 from non-diapausing *M. sanguinipes* from Arizona and maintained as such over the decades mostly on an artificial diet, supplemented with head lettuce. Between 2000 and 2005, the colony was hybridized with individuals from the Agriculture Agrifood colony in Saskatoon, Canada. In approximately 2005 and 2013, genetic material was added to the colony by mating with field-collected female non-diapausing *M. sanguinipes* collected from Arizona. Starting in 2017, the colony was moved to Arizona State University with funding from the USDA's nearby Science and Technology Phoenix Laboratory for the purpose of local lab experiments. The colony has been kept at 32.2°C during the day and 25°C at night, and the humidity fluctuates from 20–50% RH with a 14h:10h light/dark cycle. The colony is reared on a combination of organic romaine lettuce, wheatgrass, and wheat bran. Overall, the lab colony had access to a wide range of protein and carbohydrates: two food sources were carbohydrate-biased and the third was protein-biased. The mature wheat grass available to the colony was analyzed using a phenol-sulfuric acid carbohydrate assay (DuBois et al. 1956), and the protein content was determined using the Bradford protein assay (Bradford 1976) and found to be 27.62% ± 6.467 protein (Mean % ± SEM) and 14.24% ± 1.78 carbohydrate (Brosemann et al. unpubl. data). Reviews of USDA databases show that the romaine lettuce is approximately 1.24% protein and 3.24% carbohydrate, and the wheat bran is approximately 15.6% protein and 64.5% carbohydrate (FoodData Central 2021b).

Self-selected IT and performance curves.—We determined the self-selected IT and performance of the lab colony using choice and no-choice diet experiments split into three consecutive blocks using three consecutive cohorts of fifth instar nymphs. Each block contained all treatment groups for the choice and no-choice experiments, with eight grasshoppers per treatment group (four males and four females) for a total of 56 grasshoppers in each block and a total of 168 grasshoppers for the full experiment (24 grasshoppers in each treatment). Grasshoppers were removed from colony cages during the 4th instar stage and provided the same food from the colony cages until they molted into 5th instars. On the first day of the 5th (final) instar, grasshoppers were placed into the experiment.

The experiments were run in an environmental chamber kept at 32.2 °C during the day and 25 °C at night, and the humidity fluctuated from 20–50% RH with a 14h:10h light/dark cycle.

For the lab choice diet experiments, we had two treatments: Treatment A: 7p:35c and 28p:14c, and Treatment B: 7p:35c and 35p:7c. For the lab no-choice diet experiments, we restricted individual grasshoppers to one of the five isocaloric diets (7p:35c, 14p:28c, 21p:21c, 28p:14c, and 35p:7c). We weighed grasshoppers and placed them in individual perforated plastic cages (18.891 cm × 13.494 cm × 9.525 cm) with a similar set-up to that used to measure the field population IT. The rest of the methods are identical to the field population IT, with the exception that the experiments ran for 14 days, and food was changed every 3 days.

For the performance analyses, the specific growth rate (μ) was calculated for each grasshopper using the following formula: $\mu = \ln (M_1/M_2)/dt$, where M_1 is the initial mass of the grasshopper, M_2 is the final mass of the grasshopper, and dt is the days between weight measurements. Total days survived and total days spent in the 5th instar prior to molting to an adult were calculated. The proportion of grasshoppers surviving or molted was calculated for each day of the experiment.

Statistical analyses.—We tested all data for assumptions of normality and homoscedasticity implicit in parametric tests. We transformed any of the data that did not meet these requirements prior to analyses, or non-parametric analyses were used. Outliers were removed from the analyses. We performed analyses for ITs using IBM SPSS Statistics 24 (2017), with all other analyses performed using R 3.5.1 (2020). To determine IT differences among different populations, we used generalized additive models to detect nonlinear trends as discussed by Lawton et al. (2021), which ultimately resulted in a generalized linear model (family: multivariate normal distribution, link: identity).

Results

Field population studies

Plant collection.—The Bliss location was primarily composed of dead vegetation cover, with some live vegetation in each sample plot. The average percent ground covered by dead and living grasses was 57.4 ± 12.137 (Mean % ± SD), the average percent ground covered by dead and living forbs was 0.6 ± 0.548, and 2–15% ground covered by dead and living shrubs when shrubs were present (Table 1). The Boise location consisted of more live vegetation than the Bliss location. The average percent ground covered by dead and living grass was 39 ± 12.942, the average percent ground covered by dead and living forbs was 25 ± 11.726 (Mean % ± SD), and there were no shrubs present at this site (Table 1).

Intake targets.—Both field populations (Bliss and Boise, ID) of grasshoppers ate non-randomly from the two diet dishes. There was a significant interactive effect of sex and treatment on carbohydrate and protein consumption for the Bliss population, but no significant effect on the Boise population. The Boise, population tended to regulate its IT more tightly (Fig. 1, Table 2). The ITs of both field populations were carbohydrate-biased, with population 1 consuming 1p:3.5c and population 2 consuming 1p:2.1c (Fig. 2A, B).

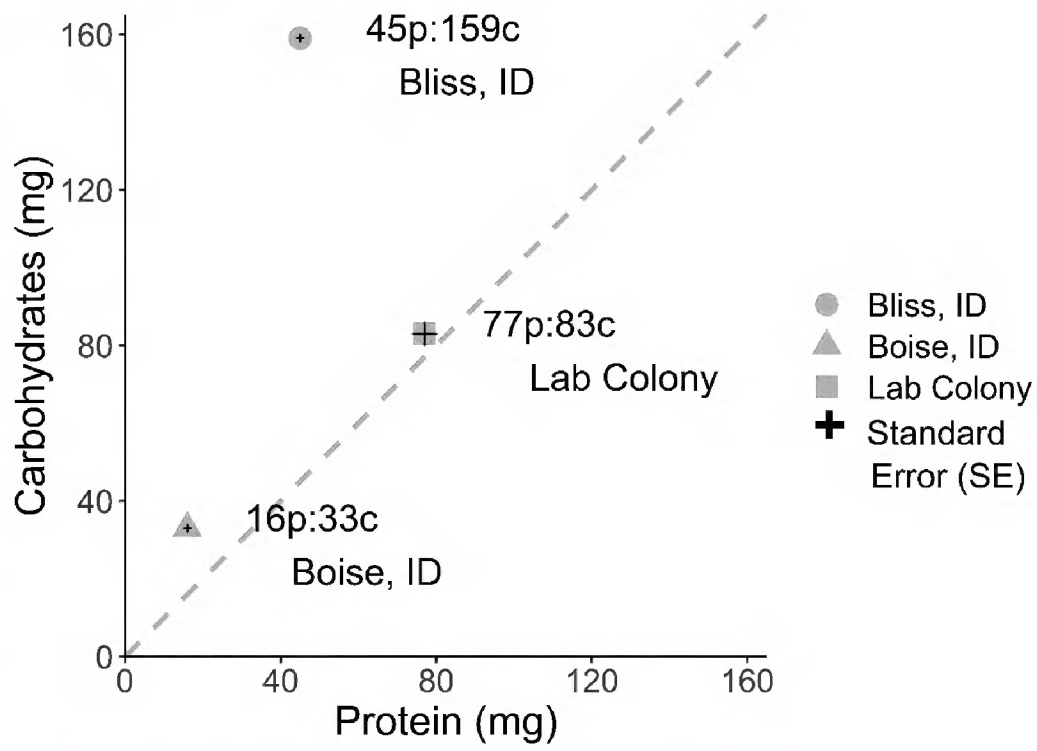

Fig. 1. Field populations and lab population ITs. Average intake target (+/- SEM) for two field populations, Bliss and Boise, ID, and the lab colony. The dashed line represents a 1:1 ratio of protein and carbohydrates, and the crosses on the data points represent SE.

Chemical analyses.—The macronutrient ratios of the sampled plants in the Bliss and Boise locations were close to the self-selected ITs for both populations, as indicated by the small Euclidean distances between the sampled plants' p:c ratio and the IT (Average Euclidean distances of combined plants ± SE: Population 1 = 0.021 ± 0.006; Population 2 = 0.010 ± 0.002). Using a Wilcox rank-sum test, we found there was no significant difference in the average Euclidean distances, calculated between the sampled

Table 1. Field sites. Habitat and environmental data from field plots in Idaho (see Suppl. material 1: Figs S6–S17 for maps and habitat plots). Plot location coordinates are based on WGS84.

Plot	Date	Time (PM)	Latitude, Longitude	Temp °C	RH %	Wind m/s	Live Veg %	Total Veg %	Rock %	Litter %	Dung %	Grasses % Ground Cover	Forbs % ground cover	Shrubs % ground cover
Bliss, ID 1–1	26-Jun	12:00	42.981492, -114.9288965	26.1	26.1	4.8	<5	75–100	0	0	<5	74	1	0
Bliss, ID 1–2	26-Jun	12:25	42.9813708, -114.929146	26.3	22.9	5.5	<5	50–75	<5	0	<5	59	1	0
Bliss, ID 1–3	26-Jun	12:50	42.9814282, -114.9310661	27.1	18.8	6.0	<5	50–75	<5	0	0	55	0	2 (dead)
Bliss, ID 1–4	26-Jun	1:05	42.9811249, -114.9307657	28.5	18.1	4.6	5–25	50–75	0	0	<5	40	0	15
Bliss, ID 1–5	26-Jun	1:30	42.9799997, -114.9294353	28	17.8	5.2	<5	50–75	0	0	<5	59	1	0
Boise, ID 2–1	2-Jul	1:00	43.3943539, -115.9510955	22.7	28.7	4	<5	50–75	0	0	0	55	5	0
Boise, ID 2–2	2-Jul	1:20	43.394394, -115.9512032	24	28.6	4.6	25–50	75–100	0	0	0	50	30	0
Boise, ID 2–3	2-Jul	1:40	43.3944951, -115.9512009	23.5	28.7	4.5	25–50	50–75	0	<5	0	30	30	0
Boise, ID 2–4	2-Jul	2:00	43.3946555, -115.9525402	23.4	26.7	6	25–50	50–75	0	<5	0	25	35	0
Boise, ID 2–5	2-Jul	2:15	43.3940407, -115.9512009	24.2	23.4	5.3	25–50	50–75	0	<5	0	35	25	0

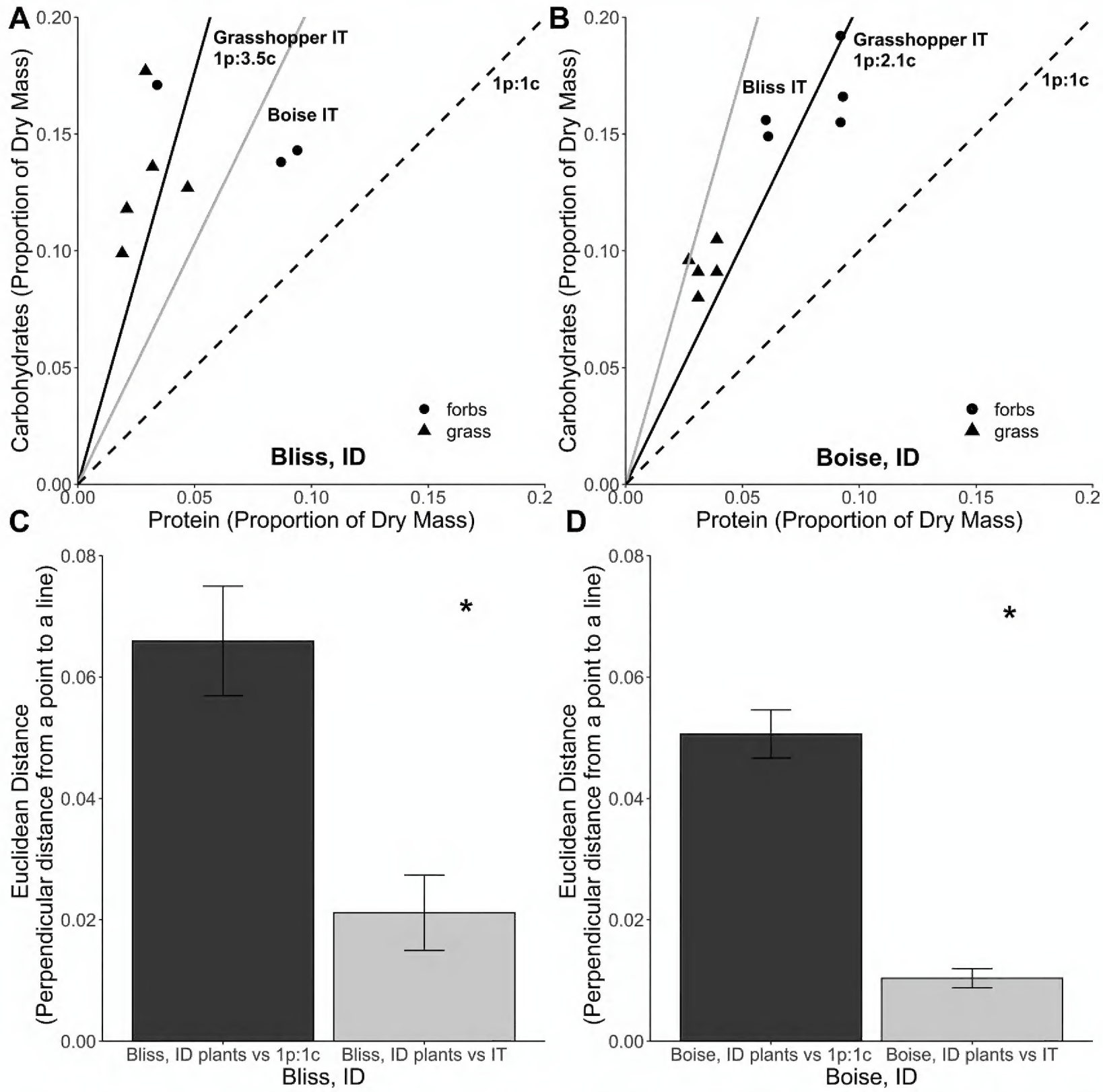

Fig. 2. Field IT compared to nutritional landscape. **A, B.** Grasshopper intake targets of the field populations (black solid line) alongside the nutrient contents of grasses (triangles) and forbs (circles) collected from the same fields. The grey solid line represents the intake target from the other field population. The dotted line represents a 1p:1c ratio. **C, D.** The average Euclidean distance between the plants (triangles and circles in A and B) and either the grasshopper IT from each location or the 1p:1c line. * denotes a significant difference between the Euclidean distances calculated from the IT and the 1p:1c line.

plants and the IT (Fig. 2A, B), between populations 1 and 2 (w = 53 p = 0.274). We found that when comparing the Euclidean distance of the plants calculated with the population IT versus calculations using the 1p:1c ratio, there was a significant difference in the Euclidean distances. In this case, the Euclidean distance of the plants was lower when calculated to the population IT than to a 1p:1c ratio for both Bliss (t = -4.0827 df = 14 p = 0.001) and Boise (t = -9.464 df = 11.773 p = $7.536^{e\ -07}$) field sites (Fig. 2C, D), suggesting that the sampled plants macronutrient rations were closer to the IT than to a balanced ratio.

Lab studies

Lab self-selected intake targets.—We calculated ITs for each of the three blocks of the experiment, and t-tests were used to determine if both treatment groups were regulating consumption or eating randomly and were compared to each other. Grasshoppers given Treatment A ate significantly different portions from the high carbohydrate and high protein dishes, overall consuming slightly more from the high protein dish, and appeared to regulate their consumption (Table 3). Grasshoppers given Treatment B ate equally from both dishes, but grasshoppers from both treatments arrived at similar p:c ratios (Table 3). We used a full MANCOVA with sex and diet pairing as independent variables and total carbohydrates and protein eaten as separate dependent variables. We included block as a random factor. There was a main effect of diet treatment (group) and block (Table 2). For simplicity, we report the overall ITs for males and females combined in Fig. 1, which was 0.77 mg (+/-3) protein to 83 mg (+/-3) carbohydrates. We also used generalized linear model methods to determine if the ITs of our lab colony were significantly different from ITs of the Bliss and Boise populations. Using the first three days of the lab colony IT experiment, we found that our lab colony's carbohydrate and protein consumption was significantly different from the Bliss population, but not the Boise population (Suppl. material 1: Table S1). We found that the Bliss population was consuming more carbohydrates and protein than both the Boise population and our lab colony (Suppl. material 1: Figs S1–S4).

Table 2. IT Statistics. MANCOVA statistics for field and lab intake target (IT) studies testing the effects of sex, diet treatments, and cohort (lab only) on the total amount of protein and carbohydrates consumed.

Population	Effect	Pillai's trace Value	*F*	Error df	Sig.
Bliss, ID	Intercept	0.972	364.1	21.000	0.000
	Initial mass	0.146	1.792	21.000	0.191
	Sex	0.255	3.599	21.000	0.045
	Diet pair	0.662	20.580	21.000	0.000
	Sex * Diet pair	0.008	0.086	21.000	0.918
Boise, ID	Intercept	0.037	0.774	40.000	0.468
	Initial mass	0.341	10.330	40.000	0.000
	Sex	0.008	0.155	40.000	0.857
	Diet pair	0.126	2.890	40.000	0.067
	Sex * Diet pair	0.005	0.108	40.000	0.898
Lab Colony	Intercept	0.474	13.070	29.000	0.000
	Initial mass (covariate)	0.029	0.438	29.000	0.649
	Sex	0.152	2.606	29.000	0.091
	Cohort	0.510	5.141	60.000	0.001
	Diet pair	0.215	3.964	29.000	0.030
	Sex * Cohort	0.029	0.220	60.000	0.926
	Sex * Diet pair	0.033	0.502	29.000	0.610
	Cohort * Diet pair	0.074	0.578	60.000	0.680
	Sex * Cohort * Diet Pair	0.212	1.783	60.000	0.144

Lab performance.—Using the no-choice experiments, we determined the specific growth rate (Fig. 3A) and absolute growth rate (Suppl. material 1: Fig. S5), as well as the proportion of individuals surviving and successfully molting on diets that differed in p:c ratio. Because the data did not meet the assumptions for an ANOVA, we used the non-parametric Kruskal-Wallis test to determine if there was a significant effect of diet on specific growth rate (χ^2 = 32.41, df = 4, p = 1.576, e $^{-06}$). We used the pairwise Mann-Whitney non-parametric post hoc tests to determine that there were no significant differences between all the treatment groups, except 7p:35c, which was significantly lower than all other treatments (Fig. 3A).

We analyzed the final proportion molted and proportion survived using Fisher's exact test of independence since grasshoppers were removed from the experiment after they had either molted or died. There was no significant difference in survival among the treatment groups (p = 0.4298). However, there was a significant difference among treatment groups regarding the final proportion of grasshoppers successfully molted (p = 0.003), with the 7p:35c treatment group being significantly different from all other diet treatments. Overall, diet treatment 7p:35c had the lowest proportion of grasshoppers survive and molt (Fig. 3B–C). All diet treatments except 7p:35c had a large increase in molts by day 6 or 7, whereas diet treatment 7p:35c delayed molting (Fig. 3C).

Discussion

Our long-term lab colony selected a balanced 1p:1c IT, which is similar to previous studies using first (1p:0.96c; Behmer and Joern 2008) and second (1p:0.90c and 1p:0.95c; Fielding and Defoliart 2008) generation lab-reared *M. sanguinipes*. Our lab colony performance experiments supported our hypothesis that *M. sanguinipes* selects an IT range that aligns with high performance, similar to Behmer and Joern (2008) and Fielding and Defoliart (2008). In contrast with the lab populations, we found that *M. sanguinipes* collected directly from field populations had carbohydrate-biased ITs (1p:2.1c and 1p:3.5c). The field populations may have shifted their ITs to better match their nutritional landscape and/or in response to disease, elevated activity, or other environmental factors (Fig. 2). For example, the Boise landscape had a higher representation of forbs than Bliss, ID, which may have contributed to the slightly less carbohydrate-biased IT of that population (Table 1); further studies are needed to disentangle these potential hypotheses. Understanding how these factors impact ITs will be key to predicting the nutritional physiology of these organisms in different environments, which, in turn, may assist in the development of novel management methods.

Table 3. IT paired t-tests to determine if there was equal consumption from both diets in each treatment group.

Population	Paired t test	*t*	*p*	df
Bliss, ID	a 7p:35c + 28p:14c	112.520	<0.001	12
Bliss, ID	b 7p:35c+ 35p:7c	123.330	<0.001	13
Boise, ID	a 7p:35c + 28p:14c	-20.384	<0.001	22
Boise, ID	b 7p:35c+ 35p:7c	-51.120	<0.001	22
Lab	a 7p:35c + 28p:14c	-4.008	0.006	21
Lab	b 7p:35c+ 35p:7c	-0.008	0.994	20

There is some evidence from lab-based experiments that populations either adapt or acclimate to their nutritional environment by matching their IT and performance to their ancestral diet (Raubenheimer et al. 2012). For instance, as mentioned briefly earlier, *P. xylostella* moths reared on a single homogenous food with a fixed nutrient composition for about 350 generations exhibited a strong selection for the same nutrient balance as their ancestral colony diet and had a sharp decline in performance when they deviated from that macronutrient balance, showing an extreme food specialization (Warbrick-Smith et al. 2009). A prior study reared the same species for multiple generations on either carbohydrate-rich or poor foods. The selected lines developed the capacity to minimize or maximize body fat accumulation to improve fitness when confined to their treatment diet (Warbrick-Smith et al. 2006). The diets did impact host plant preference for egg laying, but the authors did not test whether the selection experiment shifted ITs.

Results from field-based research, on the other hand, suggest that aligning ITs and performance to match the nutritional landscape is uncommon in the absence of long-term specialization and that physiological status is a better predictor of IT than ambient plant nutrient contents. For example, in West Africa, *Oedaleus senegalensis* (Krauss, 1877), the Senegalese grasshopper, did not shift its IT to match seasonal shifts in plant p:c; instead, ITs correlated poorly with plant nutrients and varied with age and sex (Le Gall et al. 2021). In Australia, a comparison of a non-migratory and two migratory grasshopper species through space and time revealed that populations of the non-migratory grasshopper had different ITs through space, but it was likely to redress nutrient imbalances from the local environment rather than to match them (Lawton et al. 2021). The migratory species largely maintained the same IT, even when there was a mismatch between their IT and their nutritional landscape, similar to Senegalese grasshoppers (also a migratory species).

In Paraguay, field populations of *Schistocerca cancellata* (Serville, 1838), the South American locust, maintained a carbohydrate-biased IT and only gained mass when fed the most carbohydrate-biased plants, despite being in a quite protein-biased landscape (Talal et al. 2020). This result corroborates earlier re-

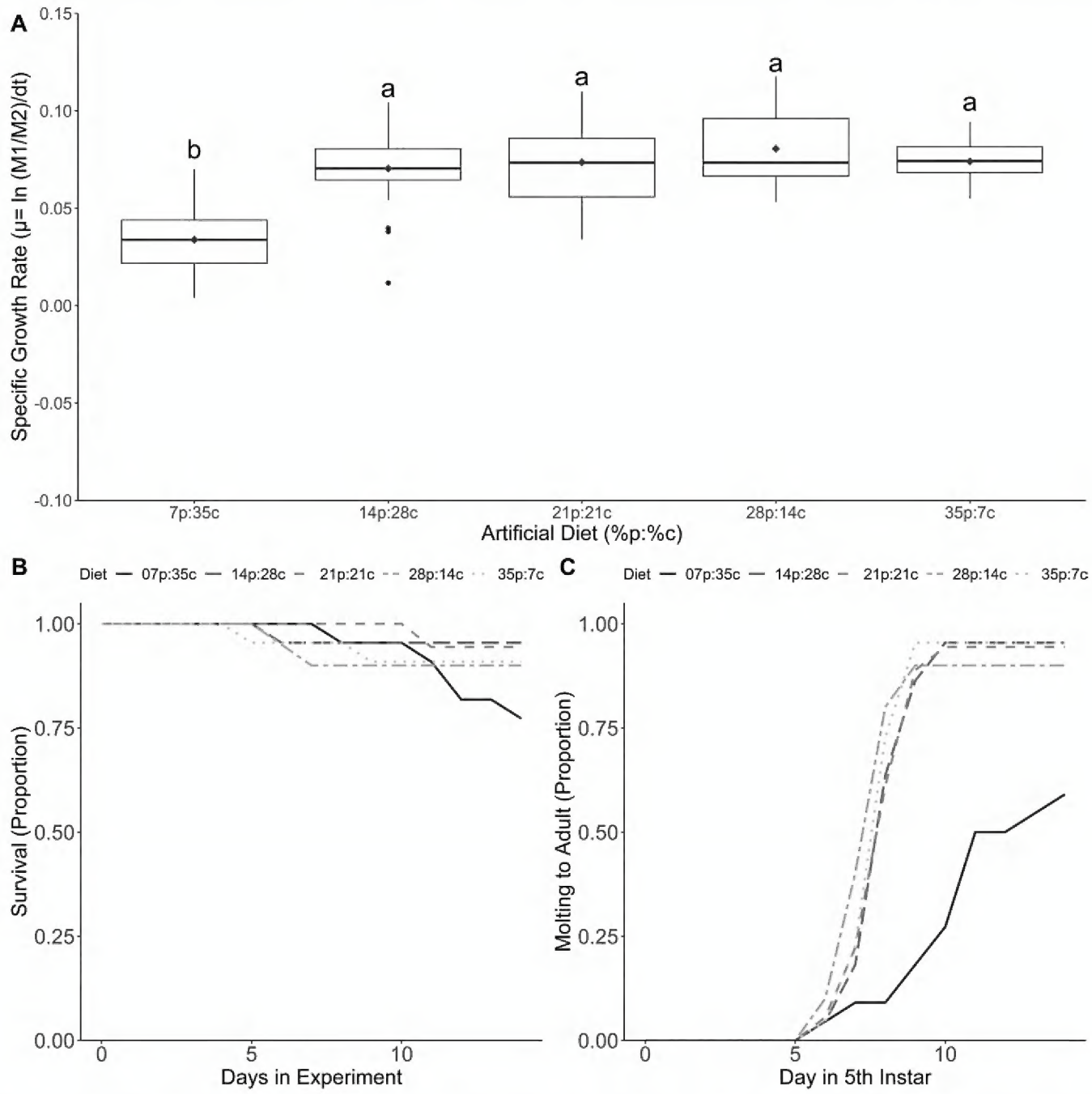

Fig. 3. Performance experiments. Survival and specific growth rates of grasshoppers from the long-term lab colony no-choice diet experiments. **A.** The specific growth rates for each diet treatment. Diamonds indicate the mean and bolded lines indicate the median. Boxes are +/- 25%, lines represent minimum and maximum values excluding extreme values, and dots indicate data points > 1.5 farther from the box edge than the interquartile range. Lower case letters indicate differences from Mann-Whitney post-hoc analyses. **B.** The proportion of grasshoppers surviving through time on each diet treatment. Most diet treatments did not have individuals die until the 5th day of the experiment, and most treatments except 7p:35c had minimal deaths (although there were no significant differences among treatments). **C.** Proportion of grasshoppers molting to adults over time. Most of the diets saw increases in molting from days 5–7, except diet treatment 7p:35c, which was delayed and had the least number of grasshoppers successfully molt (significantly different from all other treatments).

search indicating that locusts and migratory grasshoppers require a carbohydrate-biased diet to undergo long-distance migration (Cease et al. 2017) and that low p: high c environments support population growth (Cease et al. 2012, Word et al. 2019, Le Gall et al. 2020a, b). In the face of shifting environments, organisms and populations will acclimate, evolve, move, or perish. Collectively, these studies suggest that migratory species may rely on migration or post-ingestive mechanisms to regulate nutrient balance in the face of environmental change and that physiological constraints in nature limit matching a population's IT to its nutritional landscape except when under strong selection.

The current study using the migratory grasshopper provides some support for both non-mutually exclusive hypotheses: that population IT is shaped by local nutritional landscape and by physiological status. Under standard rearing conditions, the colony has *ad libitum* access to foods encompassing a broad macronutrient range: wheat seedlings (1.9p:1c), romaine lettuce (1p:2.6c), and wheat bran (1p:4.1c) (Brosemann et al. unpubl.; FoodData Central 2021a). Therefore, it is unlikely that there was strong selective pressure to develop a narrow IT based on the lab diet, in contrast to the long-term moth colony reared on a single food choice (Warbrick-Smith et al. 2009). The lab colony likely arrived at a 1p:1c IT (Fig. 1) because it maximizes performance in a lab colony. While there was not a narrow performance peak, the IT was within the range where the lab colony maintained a high growth rate and fast development time across the 1:1, 1:2, 2:1, and 5:1 p:c diets (Fig. 3).

The field populations both had carbohydrate-biased ITs that matched their local environments. Although the 1p:2c Boise population IT could have been reached based on the plants available in both field environments, the 1p:3c IT that the Bliss population selected could only have readily been reached in the Bliss location (Fig. 2). Furthermore, neither field environment would have supported populations to select for the 1p:1c IT that the lab population selected. The Boise location had an average of 25% forb ground cover, and the Bliss location had <1% (Table 1), indicating that the few forbs closer to 1p:1c were sparse in the landscape and that the Bliss population was in an extremely carbohydrate-biased landscape. Therefore, it is possible that the grasshopper field populations, particularly for Bliss, were under some selective pres-

sure to have carbohydrate-biased ITs to align with their nutritional landscape. However, all tests of lab colony ITs of *M. sanguinipes* nymphs performed to date resulted in a narrow range (1p:0.90c to 1p:1c) regardless of being first or second generation, being in a colony since 1970, or being originally collected from Alaska, Idaho, Nebraska, or Arizona (Behmer and Joern 2008, Fielding and Defoliart 2008; Fig. 1). Therefore, it is unlikely that the alignment between IT and local plant nutrients that we measured in this study represents local adaptation, though it could be evidence of an evolved ability to plastically respond to a restricted diet.

Many environmental factors can influence herbivore physiology and result in shifting the IT, such as activity level and pathogens. For example, *Locust migratoria* (Linnaeus, 1758), the migratory locust, increased carbohydrate, but not protein, consumption following 120 min of tethered flight (Raubenheimer and Simpson 1999). Nutrient balance affects insect immune function, and thus their ability to survive sickness and infections (Ponton et al. 2011a, b; Graham et al. 2014, Deans et al. 2017). Different immune components may be heightened by diets with different macronutrient contents, as was the case for *Spodoptera littoralis* (Boisduval, 1833) caterpillars (Cotter et al. 2011). Furthermore, Graham et al. (2014) found that Australian plague locusts that selected more carbohydrate-biased diets were better able to fight infections from the fungal pathogen *Metarhizium*. ITs that are highly carbohydrate-biased, such as we observed in our study's Bliss, ID population, could be indicative of grasshoppers selecting this diet to fight sickness or infection. Indeed, we found that the Bliss population suffered significant mortality during the experiment and prior to the start of the experiment. When we completed the setup of the Bliss population experiment, approximately 30% of the grasshoppers we had collected the previous day were dead. The Bliss population also had more cases of grasshoppers losing mass than the Boise population. While not conclusive, these signs indicate that the population may have been suffering from pathogens or parasites. Further studies on field populations are needed to determine if the selected ITs maximize performance in those conditions, as well as the potential mechanisms driving variation in population ITs. However, our data suggest that, at least for these populations, they could achieve their preferred p:c ratio locally.

Understanding the nutritional requirements of rangeland grasshoppers is important not only for understanding what types of vegetation grasshoppers will be most likely to eat but also for developing novel management strategies. For example, the balance of macronutrients is important for immune function in insects and may be important to consider when biopesticides are used for management (Lee et al. 2008, Ponton et al. 2011a, b, Deans et al. 2017, Tessnow et al. 2018). Insects that can meet their ITs in their nutritional landscapes are likely to be less susceptible to biological control strategies—either less susceptible to pathogens or less susceptible to toxins produced by the biological control agent (Graham et al. 2014, Deans et al. 2017, Tessnow et al. 2018). There is evidence that for some insects, nutritional physiology differs between populations. Research on *Spodoptera frugiperda* (J.E. Smith, 1797), studying its susceptibility to *Bt* toxins, showed that for one population, meeting the IT actually increased that population's susceptibility to the toxins. In the other two populations, eating at the IT did not affect individuals' susceptibility to the toxins (Tessnow et al. 2021). This suggests that not only will there be differences in how IT relates to performance and survival between species, but there could also be differences among populations, so analyzing populations' nutritional physiology and ecology is critical to any management strategy. Understanding how the nutritional landscape interacts with an organism's IT and macronutrient requirements is going to be important, especially with more farmers and ranchers turning to biopesticides as means of managing grasshopper outbreaks (Gardner and Thomas 2002). Similar to how there are recommended temperature ranges across which biopesticides are most effective (McNeill and Hurst 2008, Rai et al. 2014, Kim et al. 2019), there should be guidance as to what types of nutritional landscapes will make pests most susceptible to biopesticides.

Another aspect to consider is how biopesticide treatment might affect pest host plant preference, as it could cause the target pests to consume crops and other plants it might not normally otherwise. Biopesticides aside, knowing how pests respond to nutritional landscapes can open pathways for population suppression through agricultural practices. For example, for locusts and migratory grasshoppers that thrive in low nitrogen environments (Cease et al. 2012, Word et al. 2019), the nutritional landscape could be altered through soil amendments, crop rotations, or other practices that increase soil organic matter and nitrogen availability; this would, in turn, increase the plant protein: carbohydrate ratio and suppress pest populations (Cease et al. 2015, Word et al. 2019). To support the development of sustainable management options, future research should study how biopesticide challenges affect the nutritional demands of *M. sanguinipes* and if this species can alter its diet to decrease its susceptibility. As with the Australian plague locust, such research would add greater understanding to the potential relationship between the nutritional physiology of grasshoppers and biopesticide efficacy, leading to more diverse, sustainable, and efficient management options.

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Supplementary material 1

Author: Deanna Zembrzuski, Derek A. Woller, Larry Jech, Lonnie R. Black, K. Chris Reuter, Rick Overson, Arianne Cease

Data type: Environmental data

Explanation note: **Table S1.** Field sites. Habitat and environmental data from grasshopper field study plots in Idaho. Plot location coordinates are based on WGS84. **Field Diet Choice Data Set.** Diet choice experimental data from Field locations in Boise and Bliss Idaho. **Lab Diet Experiment Data Set.** Lab Diet choice and restricted diet experimental data sets. **Plant Macronutrient Data.** Data set with the carbohydrate and protein content of plants sampled from the field sites in Boise and Bliss Idaho. **Supplementary figures and tables covering additional data.**

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